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SEX-LIMITED AND SEX-LINKED INHERITANCE

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Darwin used the expression "inheritance as limited by sex" to include all cases in which a character is peculiar to one sex. His list of such cases covers in the main the group of secondary sexual characters. Darwin's expression has been contracted to sex-limited inheritance, and is widely employed to-day in the same general sense in which Darwin used the expression. For instance, Bateson in his book "Mendel's Principles of Heredity" includes both horns in sheep and color blindness in man as sex-limited characters.[1]

Now that the inheritance of several of these cases has been definitely worked out, it has become increasingly evident that such characters as color blindness, and hæmophilia in man, the twenty-five "sex-linked" characters in Drosophila, and certain characters in birds and in butterflies follow a law of inheritance that is essentially different from that followed by some of the other cases. It has become necessary, therefore, to recognize two groups of cases that differ fundamentally in regard to their heredity. To one of these groups I have applied the term sex-linked inheritance, and, for the present at least, we may still make use of the older expression sex-limited inheritance (and

[1] See pp. 169–174 in section headed "Heredity Limited by Sex; the Horns of Sheep," where the term sex inheritance limited descent (p. 172) also appears.

sex-limited character) to cover that class of cases (obviously a very mixed one which will be broken up as our knowledge regarding it becomes more certain) that includes largely, as originally intended, the secondary sexual characters.[2] In those cases of sex-linked inheritance, in which the male is heterozygous for the sex factor, the grandfather transmits his peculiarity, through his daughters, to half of his grandsons only; and reciprocally an affected female transmits her peculiarity to all her sons, and, through her sons bred to her daughters, to half of her granddaughters and to half of her grandsons[3]. Moreover the appearance of the character in the female is not exceptional or abnormal, as is sometimes implied in cases like color blindness in man, for, the character can always be transferred from the male to the female by suitable crosses.

On the other hand, there are cases in which a character appears in one sex only—the character is limited, therefore, to the male or to the female. Such cases may be properly called sex-limited, and were so called by Darwin. As typical examples I may cite the horns of certain races of sheep that are present in the ram and absent in the

[2] G. H. Shull has recently said (*Zeit. Ind. Abst. und Vererb.*, XII, 1914, p. 160) that, in his opinion, it would be better to retain the term sex-limited for those cases that I call sex-linked and call other cases secondary sexual characters. This view is not historically in accord with Darwin's usage of the term "limited by sex." This fact, in itself would be a sufficient argument for rejecting Shull's suggestion, but, in addition, the term sex limited is an actual misnomer for the class of cases to which he proposes to apply it. There are cases like the eosin eye of *Drosophila* that differ in the male and female in the same way as do many secondary sexual characters (in fact they are such in a descriptive sense) but nevertheless show sex-linked inheritance. Since a new name is required to express our fuller information in regard to some of the characters that were originally included under the older term, why not begin by adopting suitable and expressive ones.

[3] In those cases in which the female is heterozygous for a sex factor, as in birds and in butterflies, the same principle is involved but the sequence is, in a sense, reversed; thus the grandmother transmits, through her sons, her peculiarity to half of her granddaughters; and reciprocally, the affected male transmits his peculiarity to all of his daughters, and, through his daughters bred to his sons, to half of his grandsons and to half of his granddaughters.

ewe (or else more developed in the ram than in the ewe); the color of butterflies like *Papilio Memnon,* with three types of females; and the dark spot on the abdomen of the male of the bug *Euchistus variolarius.* These characters can not be transferred through the gametes to the female of their own race by any known combination.

Whether one likes or does not like the particular terms used to denote these two classes of cases, the fact remains that there are two such categories, and to ignore their existence is only to make obscure a distinction that is perfectly plain.

Concerning the mechanism involved there is something more that may be said. It has been sufficiently shown in the case of sex-linked inheritance that the sex-linked character follows the known distribution of the sex chromosomes. It is unnecessary to repeat here the abundant evidence in support of this statement. The simplest interpretation of this known relation is that the character is dependent for its realization on the sex chromosomes. I do not mean, of course, that the sex chromosomes alone produce the character but that something in these chromosomes, some "factor," acting in conjunction with the rest of the cell, conditions the character.

On the other hand, in the case of sex-limited characters the facts can not be explained on the assumption that the characters follow the *sex chromosomes.* It is clear that they do not do so. But we can give a consistent interpretation of the facts if we assume that sex-limited characters follow the distribution of the ordinary chromosomes.

Since this relation has recently been not understood and misinterpreted I may be pardoned, I hope, for taking up the question once more.

Wood crossed horned Dorset sheep with hornless Suffolks. The sons had horns, the daughters lacked them. Inbred these gave in the F_2 generation—horned ♂, 3; hornless ♂, 1; horned ♀, 1; hornless ♀, 3. Bateson and Punnett have shown that the results are explicable on the basis that one factor for horns in the male produces

horns but one factor is insufficient in the females. This conclusion was put to the test by breeding an F_1 hornless ewe to a hornless ram. The F_1 ewe should be heterozygous for the factor for horns, and, therefore, when she is bred to a homozygous hornless ram, half of her offspring should be heterozygous for hornlessness and half homozygous for hornlessness. Since half of her sons should have a factor for horns they are expected to develop horns, and this is what occurred. Half of the daughters also should have a factor for horns, but should not develop horns, and this also was true.

It has been recognized *for several years* that this and related cases can not be explained on the assumption that the factors involved are carried by the X or by the Y chromosomes. But we can interpret the statement that one factor for horns is sufficient in the males to call forth horns, but not sufficient in the female "in terms of chromosomes," if a factor for horns is carried by one of the chromosomes other than the sex chromosome. In other words we need only appeal to a mechanism with which we are familiar to cover the results.

The second illustration is furnished by the recent experiments of Foot and Strobell, and since the authors have rejected the chromosome hypothesis as inapplicable to their results, and since in the case of insects the conditions are simplified because castration experiments have shown that the sex glands are not themselves responsible for the secondary sexual characters, we may profitably consider this case even more fully.

In one of the bugs, *Euchistus variolarius,* the male has a black spot on the abdomen. The female lacks the spot. A female of this species was crossed to a male of another species, viz., *Euchistus servus,* having no spot in either sex. The daughters had no spot, the sons had a spot fainter than that of *variolarius*. Inbred these gave, in F_2, 249 females without a spot, 107 males with a spot (developed to different degrees) and 84 males without a spot. The F_1 results show that one factor for spot in the male

suffices to call forth in some degree the spot in the hybrid. Its intensity varies from a condition approaching that in pure *variolarius* to a faint spot (possibly even to no spot at all). The F_1 results show also that a single factor in the female fails to cause the spot to develop in that sex. In the F_1 male the failure of the spot to reach in most cases its full development shows obviously that the same conditions that produce a male that is perfect so far as his sex gonad is concerned, do not suffice to cause the full development of the spot, although the factor for the spot is present in one dose at least. The only confusion that is liable to arise is that in none of the F_2 females did the spot appear, although in some of them there must have been a double dose of spot. But the difficulty is imaginary as a little thought will show. In the first place the female of *E. variolarius* herself does not show the spot, *yet this female must have a double dose of spot if spot is in the X chromosome or in any other chromosome* (*except the Y*). Foot and Strobell by an elaborate analysis of the case show that the factor can not be carried by either the X or the Y chromosome. It is unnecessary to repeat their argument; for, if the factor were carried by the X chromosome, only half of the grandsons should show it, while, in fact, many more than half of them show it; and it could not be carried by the Y chromosome because the Y chromosome of *variolarius* is not present in the female, hence could not have entered the cross as made. We are concerned then only with a third possibility, viz., that there is something in the female condition itself that is inimical to the development of the spot. *Since neither X nor Y carries the factor in question it must be present in duplex in the female of variolarius* (*if every gamete must have it in simplex and the experiment shows that this is the case*), *and since the spot does not show in the female of variolarius, it is obvious that it can not appear in that sex even in duplex. If it be granted that the character is like other Mendelian characters, and the authors' evidence show that it is inherited as are Mendelian characters, the conclusion*

is self evident; for, in demonstrating that all of the gametes of variolarius carry spot the authors actually destroy their own argument.

It only remains to point out some of the different ways in which a factor being present in duplex both in the male and in the female produces its effect only in the male. In some cases it has been shown that the ovary produces some substance that is inimical to the production of certain characters. For instance in fowls and in ducks the presence of the ovary suppresses the development of the male plumage. That the factors for the male plumage are present is shown by its development when the ovary is removed. But in some insects it has been found that neither the ovary nor the testis produces these kinds of substances; for, when the testis or the ovary is removed the secondary sexual characters are not affected. Here the mode of explanation must be different. But the conditions, or complex, or factors that produce the ovary in the female are acting in every cell of the body, and consequently an effect, that is indirectly caused in the fowl or duck, might be directly caused in the insect. For, each cell is a chemical factory. Such a factory may help to produce an ovary and the ovary produce a substance that demonstrably suppresses the male plumage, or the same kind of factory may do similar work through the activity of some other part of the body, or conceivably it may do its work in every cell of the body. This it seems to me is the most reasonable view to take of the matter in the case of the *variolarius-servus* cross. We can express the same thought in symbols by representing the female of *variolarius* by XXAABBCCDDSS, etc., and the male by XYAABBCCDDSS, etc. The chemical interaction between two X's and the rest of the cell is of such kind that it produces a female, and the female complex, as such, is inimical to the development of a spot and favorable for the development of the accessory organs of reproduction and of all secondary sexual characters of the female, while XY and the rest of the cell is inimical to the development

of the acessory organs and of the secondary sexual characters of the female, and favorable for the development of the accessory sexual organs and of the secondary sexual organs of the male. This view is of course compatible with the idea that there may be special factors for these organs in chromosomes other than the sex chromosomes, and the view holds both in a general way and on the special chromosome hypothesis as well.

To assume that all the factors for characters that are shown by the male or by the female must be carried by a sex chromosome *of some kind,* if carried at all by chromosomes, is a travesty of the point of view of those who hold to the chromosome hypothesis as a reasonable working hypothesis to account for Mendelian inheritance. Just as it has been shown that there are factors in the sex chromosomes that affect many parts of the body, that are not concerned with differences of sex; so, on the other hand, the evidence shows that there are factors in other chromosomes that are influential in producing secondary sexual characters.

INHERITANCE OF ENDOSPERM TEXTURE IN SWEET × WAXY HYBRIDS OF MAIZE

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Introduction

In a previous publication,[1] the first and second generation of crosses between sweet and waxy varieties of maize were reported and a tentative explanation of their behavior was suggested. It is now possible to add the results of the third season, which to some extent afford a test of the explanation proposed in our first publication.

The immediate result of crosses between the Chinese variety of maize having a waxy endosperm and varieties with sweet endosperm was the production of seeds having a horny endosperm indistinguishable from that of ordinary field varieties of maize. In the second xenia generation all three kinds of endosperm reappeared in the proportion of 9.20 horny, 3.95 sweet, and 2.85 waxy. This ratio was accepted as a 9:4:3 dihybrid ratio. For although the deviations of the individual ears, individual families and the totals were too large to be ascribed to chance, the deviations were not consistently in one direction and to predicate more complicated formulæ would have necessitated different assumptions for different ears. The only interest in treating the problem in this way would be that of solving a mathematical puzzle, for it would be practically impossible to secure individuals enough to test adequately the validity of the assumptions which it would have been necessary to make.

Admitting, then, that the ratios were only an approximation representing a general tendency, it became of

[1] Collins, G. N. and Kempton, J. H., "Inheritance of Waxy Endosperm in Hybrids with Sweet Corn," Circular 120, U. S. Department of Agriculture, Bureau of Plant Industry, 1913.

interest to learn whether predictions were still possible.

For the purpose of making comparisons easy, the original diagram representing the second xenia generation is here repeated. (See Fig. 1.) The meaning of the symbols is as follows: *S* is the factor for sweet, and *X* the factor for waxy. When both *S* and *X* are present the seed is expected to be horny. Small letters indicate the absence or latency of the factors.

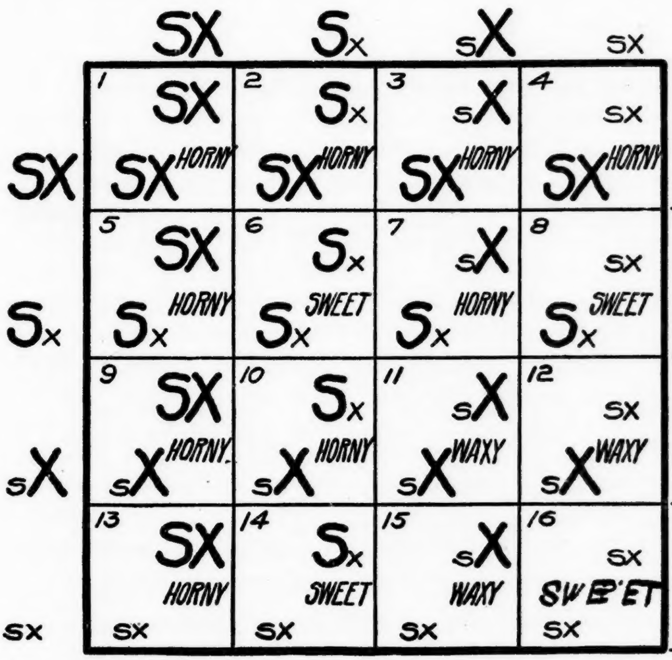

FIG. 1. Diagram showing the gametic composition of second-generation hybrids between waxy and sweet varieties of maize.

Since in both sweet and waxy the alternative factor necessary to produce horny is assumed to be lacking, the gametes produced by sweet varieties are represented by *Sx* and the gametes produced by varieties with waxy endosperm by *sX*. The synthetic horny produced by crossing waxy and sweet is then represented by a combination of

these, or $SxsX$. Assuming a chance recombination of these factors in the gametes derived from these synthetic horny seeds, the gametes will be of four kinds. Both the sweet and the waxy may be present (SX) or the sweet may be present without the waxy (Sx), or the waxy without the sweet (sX), or both may be absent (sx). At fertilization each of these kinds of gametes may unite with any one of the four corresponding kinds derived from the other parent, producing 16 zygotic combinations. In the diagram the four classes of gametes from one parent are given in the horizontal row at the top, and the same four classes from the other parent in the vertical row at the left. Each gametic combination from the top is repeated four times in the squares below, while each combination at the side occurs four times in the corresponding horizontal row of squares. Thus each of the squares represents the result obtained by combining the gametes representing the horizontal and vertical rows that intersect at that point. In all cases where both S and X occur together the seed should be horny, where only S occours the seed should be sweet, when only X occurs it should be waxy, and in one square (No. 16), where neither S nor X occurs there is a new combination which the results have shown to be a new type of sweet seed, indistinguishable from ordinary sweet seed but behaving differently when crossed with other types of endosperm.

In accordance with the above analysis the expected results in the third xenia generation were as follows:

	Proportionate No. of Ears.	Proportions of Seed Classes.
Self-pollinated horny.		
	1	All horny
	2	3 horny: 1 sweet
	2	3 horny: 1 waxy
	4	9 horny: 4 sweet: 3 waxy
Self-pollinated sweet.		
		All sweet
Self-pollinated waxy.		
	1	All waxy
	2	3 waxy: 1 sweet

Crosses between different plants from horny seeds.		
	25	All horny
	20	3 horny: 1 sweet
	20	3 horny: 1 waxy
	16	9 horny: 4 sweet: 3 waxy
Crosses between different plants from sweet seeds.		
		All sweet
Crosses between different plants from waxy seeds.		
	5	All waxy
	4	3 waxy: 1 sweet
Crosses between horny and sweet.		
	3	All horny
	6	1 horny: 1 sweet
	1	1 horny: 1 waxy
	2	3 horny: 1 waxy
	2	1 horny: 2 sweet: 1 waxy
	4	3 horny: 4 sweet: 1 waxy
Crosses between horny and waxy.		
	5	All horny
	4	3 horny: 1 sweet
	10	1 horny: 1 waxy
	8	3 horny: 2 sweet: 3 waxy
Crosses between sweet and waxy.		
	1	All horny
	1	All waxy
	2	1 horny: 1 sweet
	2	1 horny: 1 waxy
	2	1 sweet: 1 waxy
	4	1 horny: 2 sweet: 1 waxy

Third Xenia Generation

Four of the ears bearing second xenia generation seed were selected for planting in 1913, one self- and one cross-pollinated ear from each of the two hybrid families Dh 216 and Dh 221. These families were selected because in 1913 the family Dh 221 showed the greatest deficiency of sweet seeds and Dh 216 was the only family that showed sweet seeds in excess of the expected. The three classes of seeds from each of the ears were planted separately.

Unfortunately as the result of an accident crosses were not made between the plants grown from the different classes, but a total of 77 selfed ears were obtained, a num-

ber sufficient to indicate whether the initial assumption regarding the gametic compositions was of value in arranging the observed facts.

PROGENY OF SWEET SEEDS

Sweet seeds were assumed to result from squares 6, 8, 14 and 16. It will be seen that in none of these is there any factor other than *S* and since the absence of both factors, as in square 16, is also assumed to produce sweet, we should expect nothing but all sweet ears from self-pollinated plants grown from sweet seeds.

Seventeen self-pollinated ears were secured from plants grown from sweet seeds. All the seeds of these ears were sweet with the exception of one waxy seed. This one waxy seed was colored and since it occurred on an ear from a white sweet seed that otherwise produced only white sweet seeds, the exception may reasonably be ascribed to accidental foreign pollen.

PROGENY OF WAXY SEEDS

Waxy seeds were assumed to have resulted from the combinations shown in squares 11, 12 and 15. Seeds from square 11 should produce only waxy seeds. Squares 12 and 15 should produce ears with waxy and sweet seeds in proportion of 3 waxy to 1 sweet. There should, therefore, be one all waxy ear to two with both waxy and sweet seeds. There were in all 29 ears from waxy seeds, 11 of which were all waxy and 18 with both waxy and sweet seeds. The numbers are small but at least both kinds of ears were secured and the proportion does not violate the original assumption. The 18 ears with both waxy and sweet seeds all produced them in approximately the 3:1 ratio. The numbers are given in Table I. The totals with 3,154 seeds indicate that if there is a deviation, it is almost certainly less than 2 per cent.

All the sweet seeds that occur on ears grown from waxy seeds are assumed to belong to the new class of sweet seeds corresponding to that represented in square 16.

Plantings of such seeds are being made for comparison with the ordinary class of sweet seeds having the same ancestry. These are represented by the sweet seeds occurring on ears having horny and sweet seeds.

TABLE I

WAXY SEEDS SELF-POLLINATED. EARS SHOWING WAXY AND SWEET SEEDS. EXPECTED: 25 PER CENT. SWEET

Parent Ear	Pedigree Number	Total No. Seeds	No. Waxy Seeds	No. Sweet Seeds	Per Cent. of Sweet Seeds	Deviation ÷ Prob. Error
Dh 216–1 (Cross-Pollinated)	1938	301	216	85	28.2 ± 1.7	+1.9
	1939	112	85	27	24.1 ± 2.7	− .3
	1940	264	202	62	23.5 ± 1.8	− .8
	1942	18	14	4	22.2 ± 6.6	− .4
	1943	349	258	91	26.1 ± 1.6	+ .7
	1949	149	100	49	32.9 ± 2.6	+3.0
	1950	138	103	35	25.4 ± 2.5	− .2
Dh 216–2 (Self-Pollinated)	1972	389	302	87	22.4 ± 1.4	−1.9
	1973	187	136	51	27.3 ± 2.2	+1.0
	1974	174	138	36	20.7 ± 2.1	−2.0
	1975	85	67	18	21.2 ± 3.0	−1.3
	1976	34	21	13	38.2 ± 5.6	+2.4
	1977	313	232	81	25.9 ± 1.7	+ .5
	1978	109	79	30	27.5 ± 2.9	+ .9
Dh 221–2 (Self-Pollinated)	1994	136	105	31	22.8 ± 2.4	− .9
	1995	155	116	39	25.2 ± 2.3	+ .1
	1996	51	31	20	39.2 ± 4.6	+3.1
	1997	190	146	44	23.2 ± 2.1	− .9
	Total...	3,154	2,351	803	25.5 ± .5	+1.0

PROGENY OF HORNY SEEDS

From the horny seeds the expected results are more complicated. They may be tabulated as follows:

1 ear (Square 1)	with seeds all horny
2 ears (Squares 2 and 5)	with seeds 3 horny: 1 sweet
2 ears (Squares 3 and 9)	with seeds 3 horny: 1 waxy
4 ears (Squares 4, 7, 10 and 13)	with seeds 9 horny: 4 sweet: 3 waxy.

Ears were, therefore, expected in the proportion of 1 all horny ear, 2 with horny and sweet seeds, 2 with horny and waxy seeds and 4 with all three classes. Thirty ears were secured from seed classed as horny. These ears were distributed as follows: 1 all horny, 5 with horny and

sweet seeds, 3 with horny and waxy seeds, 19 with horny, sweet and waxy seeds and *2 all sweet.*

The two all sweet ears are entirely outside the expected. Their appearance may be explained on the assumption that seeds classed as horny in 1912 were in reality sweet. No microscopical examination of the starch was made and the seeds were classified on their appearance, wrinkled seeds being classed as sweet and smooth seeds as horny. The separation of horny from sweet seeds is more difficult to make than waxy from either horny or sweet.[2]

There were, however, very few doubtful seeds in the second xenia generation and in suggesting this interpretation, we may with some propriety be accused of attempting to explain away "green balls."[3]

The two all sweet ears were descendants of an ear Dh 221-2, which showed an excess of horny seeds and a deficiency of sweet. The expected number of sweet seeds in Dh 221-2, which had a total of 493 seeds, was 123 and only 106 were classified as sweet. If this deviation resulted from a faulty classification, that is, if some of the sweet seeds failed to show the characteristic wrinkled exterior, we might expect that about 17 of the 300 seeds classed as horny would produce ears with all sweet seeds. Eleven of the ears secured from horny seeds in 1913 were descendents of this ear.

The remaining 28 ears from horny seeds are distributed among the 3 classes in reasonably close agreement to the expected. Measured by Pearson's formula for the goodness of fit,[4] it appears that such a deviation might be expected once in about twenty times.

[2] The difficulty of distinguishing between sweet and starchy seeds in crosses where the starchy variety has small seeds has been pointed out by East and Hays, "Inheritance in Maize," Bull. 167, Conn. Ag. Exp. Sta., 1911, p. 40.

[3] Pearson, K., and Heron, D., "On Theories of Association," *Biometrika*, IX, pp. 309-314.

[4] *Phil. Mag.*, Vol. L, 1900, pp. 157-175. The application of Pearson's formula to data of this kind was called to our attention by Mr. G. Udney Yule.

The three ears with horny and waxy seeds produced these classes in the expected 3:1 ratio. The numbers are given in Table II.

TABLE II

HORNY SEEDS SELF-POLLINATED. EARS SHOWING HORNY AND WAXY SEEDS. EXPECTED: 25 PER CENT. WAXY

Parent Ear	Pedigree Number	Total No. Seeds	No. Horny Seeds	No. Waxy Seeds	Per Cent. of Waxy Seeds	Deviation ÷ Prob. Error
Dh 216-2 (Self-Pollinated)	1962	327	247	80	24.5 ± 1.6	.3
Dh 221-2 (Self-Pollinated)	2000	312	235	77	24.7 ± 1.6	.2
	2007	121	82	39	32.2 ± 2.9	2.5
	Total...	760	564	196	25.8 ± 1.1	.7

Four of the five ears that produced horny and sweet seeds were also as close as could be expected to the 3:1 ratio. The fifth, however, Ped. 1965, with 249 seeds, had only 19 sweet seeds or 7.6 per cent. The numbers are given in Table III. The only explanation that can be offered in connection with this exceptional ear is that suggested for the occurrence of the two all sweet ears among those grown from seeds classed as horny, namely, the existence of sweet seeds which failed to show a

TABLE III

HORNY SEEDS SELF-POLLINATED. EARS SHOWING HORNY AND SWEET SEEDS. EXPECTED: 25 PER CENT. SWEET

Pareut Ear	Pedigree Number	Total No. Seeds	No. Horny Seeds	No. Sweet Seeds	Per Cent. of Sweet Seeds	Deviation ÷ Prob. Error
Dh 216-1 (Cross-Pollinated)	1965	249	230	19	7.6 ± 1.1	16.0
Dh 216-2 (Self-Pollinated)	1979	442	344	98	22.2 ± 1.3	2.2
Dh 221-1 (Cross-Pollinated)	1988	160	121	39	24.4 ± 2.3	.3
Dh 221-2 (Self-Pollinated)	2003	175	134	41	23.4 ± 2.1	.8
	2008	179	141	38	21.2 ± 2.1	1.8
	Total...	1,205	970	235	19.5 ± .8	6.9

wrinkled surface. This explanation is rendered less probable, however, by the unusual behavior of the aleurone color in this same ear. In the previous discussion the aleurone color has not been considered. To treat of the aleurone color would naturally lead to the question of correlation between that character and endosperm texture, a subject which in these crosses is very complicated and for the treatment of which the results thus far obtained are inadequate. It may be said, however, that with the exception of Ped. 1965 the proportions of colored to white seeds in all the ears bear out the assumption that the inheritance of the aleurone color is governed by two factors, both of which must be present to produce color. In Ped. 1965, however, which was grown from a colored seed, only 23 of the 249 seeds were white. The colored and white seeds are beautifully distinct with no intermediate or doubtful seeds. The ratio of 9.2 per cent. white might be explained as an approximation to the dihybrid ratio of 6.25 per cent. but we must then admit that instead of both factors being necessary for the development of color either factor alone may produce color.

The 19 ears from horny seeds that showed all three classes are assumed to have the same gametic composition as the original second xenia generation, previously reported. The numbers are given in Table IV. The last column of the table gives the odds in 1,000 that deviations equal to those observed are not chance deviations from the expected proportions, as calculated by Pearson's formula. Thus in Pedigree 1953 the odds are 809 to 191, or practically 4 to 1, that the deviation is not the result of chance.

As in the original ears, the approximation is sufficiently close to render futile any attempt to predicate a different arrangement of factors, but many of the deviations are too large to be ascribed to chance. In the totals the sweet class is too low and the waxy too high, in fact there is no significant difference between the totals for these two classes. The deviation from the expected is, however,

largely the result of two ears Ped. 1954 and 1967, and if the explanation suggested for the two all sweet ears from horny seeds is admitted, it may also account for the deviation in these two ears. In both ears the deficiency of sweet seeds is accompanied by an excess of horny seeds, while in neither ear is there a significant excess of waxy seeds.

TABLE IV

HORNY SEEDS SELF-POLLINATED. EARS SHOWING ALL THREE CLASSES. EXPECTED: 56.25 PER CENT. HORNY, 25 PER CENT. SWEET 18.75 PER CENT. WAXY

Parent Ear	Pedigree	Total No. Seeds	Horny Seeds		Sweet Seeds		Waxy Seeds		Chances in 1000 that the Deviation is not Accidental
			No. Expected	No. Observed	No. Expected	No. Observed	No. Expected	No. Observed	
Dh 216-1 (Cross-Pollinated)	1953	39	22	26	10	5	7	8	809
	1954	350	197	236	87	36	66	78	999+
	1955	198	111	103	50	55	37	40	470
	1956	69	39	42	17	11	13	16	777
	1957	148	83	74	37	42	28	32	664
	1958	176	99	100	44	41	33	35	133
	1963	540	304	289	135	133	101	118	832
	1964	70	39	44	18	8	13	18	983
	1966	170	96	101	42	35	32	34	524
	1967	158	89	108	39	23	30	27	995
Dh 216-2 (Self-Pollinated)	1980	35	20	16	9	11	7	8	486
Dh 221-1 (Cross-Pollinated)	1985	258	145	131	65	73	48	54	784
	1986	120	67	72	30	25	23	23	443
	1987	375	211	201	94	92	70	82	716
Dh 221-2 (Self-Pollinated)	1999	77	43	42	19	16	14	19	676
	2001	27	15	15	7	7	5	5	0
	2002	118	66	71	30	29	22	18	426
	2004	134	75	81	34	29	25	24	455
	2009	79	44	48	20	10	15	21	979
	Total	3,141	1,767	1,800	785	681	589	660	999.99

With these two ears excluded the deviation in the total for the remaining 17 ears may be ascribed to chance. Tested by Pearson's formula such deviations might be expected once in about 50 times.

CONCLUSIONS

The immediate (xenia) result of crossing varieties of maize having sweet and waxy endosperm was the production of seeds with a horny endosperm resembling that of ordinary field varieties. In the second xenia generation all the ears contained seeds of the three classes, sweet, waxy and horny, in fairly definite ratios. The data were arranged in accordance with the Mendelian formula corresponding most nearly to the observed numbers.

The third generation, like the second, gave results sufficiently close to dihybrid ratios to render unprofitable the assumption of more complicated ratios. There are, however, deviations from the expected numbers of too great magnitude to be ascribed to chance.

The ratios of waxy to non-waxy seeds were regular as far as the conditions of the experiment could determine, except for a slight excess in the number of waxy seeds in nearly all the ears in which all three classes appeared (Table IV). A deviation in number of waxy seeds as large as that shown in the total would not be expected to occur as the result of chance more often than once in one thousand times.

The ratios between sweet and horny, while approximating the predicted ratios, show numerous irregularities. Wherever there is a significant deviation in the number of sweet seeds, the observed number is below the expected. Reasons are advanced for believing that the deficiency of the sweet class may result from a failure of some sweet seeds to develop a wrinkled exterior rather than from any irregularities in segregation.

The results show the value of representing the characters by gametic factors. This method provides an orderly arrangement of the facts of heredity thus far observed with respect to these characters and makes possible fairly accurate predictions regarding the genetic behavior of the various seed classes.

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A STUDY OF VARIATION IN THE APPLE

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As a rule the subject of variation in the several characters of the apple has been given but incidental attention, and that usually in connection with the study of other problems. As a result the literature on the subject is of a fragmentary character consisting usually of a few observations here and there in papers dealing with other subjects.

It is perhaps worth while to note a few of the investigations which have thrown some light in an incidental way upon the causes of variation in apples. In fertilizer tests which were made at the New York Geneva station[1] and elsewhere, no well-defined and uniform influence of the various elements of plant food upon the color could be detected, though the New York station reports more decided results in seasons when the natural conditions were unfavorable to the development of highly colored fruit. In the comparison of tillage and sod mulch in an apple orchard, also conducted by the New York Geneva station,[2] it was found that the fruit from an orchard in sod was more highly colored and matured one to three weeks earlier than that from the tilled plot, though the latter was better in quality and kept four weeks longer in common storage. The influence of the stock upon the character of the fruit is a matter of much obscurity, the investigation of which presents such difficulties that it has received little attention. The effect of pollination also is still far from settled. It was thought at one time that the characters of the fruit were profoundly modified by the pollen received by the blossom. The data on this

[1] Bull. 289.

[2] Bull. 314.

subject have been collected by Munson,[3] who found that evidence that the pollen has any direct effect upon the fruit is largely lacking. Aside, then, from indirectly modifying the size of the fruit, the influence of the pollen, in so far as our present knowledge goes, may be left out of account in a study of apple variation.

Without doubt the most noteworthy contributions to the knowledge of apple variation are the recent papers by Shaw, of the Massachusetts station, and Stewart of the Pennsylvania station. Shaw's first paper, which appeared in the Massachusetts station report for 1910, deals entirely with the variation of the Ben Davis apple. In comparing specimens grown in a number of widely separated localities it was noted that variations due to climatic condition were strongly marked and affected practically all characters of the fruit. Modifications of form were especially noticeable The depth of coloration was looked upon as correlated with latitude, being pink in the specimens from Arkansas and deep crimson in those grown farther north. The amount of overcolor seemed to be controlled by local conditions. The color was especially good in the apples from the Pacific coast and those from Colorado, Pennsylvania, and Indiana. In a given orchard temperature appears to be the most influential factor governing size. The flesh was notably white in the fruit from Colorado. The apples from Colorado and California were less firm than those from other localities. The southern-grown specimens were more juicy and of better quality than those from the north, which were apt to be dry, hard, flat, and sometimes astringent. It appears that a mean temperature of at least 60° F. for the growing season is required for the satisfactory production of the Ben Davis. The poor quality of the northern-grown specimens is apparently due to a lack of sufficient heat to properly develop the fruit.

In Shaw's second paper in the Massachusetts station report for 1911 the fact is emphasized that the grower

[3] Me. Sta. Rept. (1892), pp. 29–32.

should choose those varieties which he can grow to the highest degree of perfection under his conditions of soil and climate. The causes of variation are summarized, giving special attention to the influence of temperature as a factor in the distribution of apple varieties. The northern limit is regarded as fixed by the lowest temperature which the tree will stand, while the effect of summer heat upon the development of the fruit is looked upon as limiting the distribution southward. The elongation of the fruit was found to be correlated with a low temperature for two or three weeks after blooming. A low summer temperature produces greater acidity, higher content of insoluble solids, greater astringency, smaller size, and scalding in storage. The extent of coloration was regarded as decreasing from the center of distribution in passing either north or south, while the intensity of coloration was considered greatest in high latitudes and altitudes. Excessive summer heat results in uneven ripening, premature dropping, rotting on the tree, poor keeping quality, lack of flavor, mealiness, less intense color, and smaller size. For each variety there is a mean summer temperature at which it reaches its highest development.

It will be noted that Shaw's method of investigating the problem consisted in securing fruit for comparison from widely separated localities and attempting to correlate the various characters with the conditions of production. Stewart, on the contrary, confined his study to apples grown in one locality and noted the effect of modifying one at a time those factors within his control. This is the more scientific method of procedure, but has the disadvantage that the variations are far less striking and a smaller number of factors can be studied. An account of Stewart's experiments and the results so far attained is found in the reports of the Pennsylvania station since 1907. These papers deal largely with the effect of fertilizers and different cultural methods on the yield, color, size and growth of the apple. The various factors influ-

encing these characters are enumerated and the results are given of the studies made of them. It is noted that the factors are so interrelated that the best conditions for producing one effect are often injurious in some other direction and that the chief problem in orchard management is a proper balance of the various factors. An "optimum principle" is recognized, according to which plant growth and development increase as the most distant essential factors approach the optimum. The factor farthest from the optimum, therefore, whether below or above, may control the results from a crop

Outline of the Experiment

Since the season of 1912 was one of full crop in nearly all centers of apple production, conditions were especially favorable for the study of variation in this fruit. The writer accordingly obtained specimens for study and comparison grown in a number of localities under quite dissimilar conditions. The method employed was therefore that of Shaw, as pointed out in the last paragraph, rather than that of Stewart. The study has been pretty largely confined to Washington-grown apples, though a few have been obtained for purposes of comparison from the east and middle west. The formal investigation of the problem has been carried on but a single season, which is entirely too brief a study to demonstrate conclusively all points touched upon. The conclusions reached, however, are strongly supported by many observations in various localities extending over a number of seasons, and are so suggestive of further lines of study as to justify a report at this time.

In carrying on this investigation the aim has been to secure as much information as possible regarding the conditions under which the fruit was grown. The endeavor has been to get into communication with the growers and obtain from them through correspondence data regarding the character of the soil, rainfall, irrigation, elevation, exposure, temperature, age of trees, fertilization and

cultivation. The chief line of observation had to do with the variations which occur in the different samples of the same variety as obtained from different sources. To get at this side of the problem, careful observations were made as to the condition of the apples, and their various characters were recorded in a complete technical description of each sample for the purpose of making a comparative study of the samples of the several varieties. In addition to this written description, photographs were made showing typical specimens in various positions and when cut in cross and longitudinal sections. In general it may be said that variations are found in the form, size, color, internal structure, texture, flavor, quality, specific gravity, chemical composition, time of ripening, and keeping quality. The attempt is made to correlate these characters with the conditions of growth in so far as they are known and to work out the law of the relation of environmental factors to the characters of the fruit.

The following apples were made use of in the study: Arkansas, one sample; Arkansas Black, one sample; Baldwin, eight samples; Ben Davis, nine samples; Delicious, three samples; Esopus, seven samples; Gano, seven samples; Grimes, seven samples; Jonathan, eight samples; Lawver, one sample; McIntosh, one sample; Northern Spy, seven samples; Rhode Island Greening, three samples; Rome, eleven samples; Stayman, five samples; Tompkins King, four samples; Wagener, six samples; White Peamain, three samples; Willow, one sample; Winesap, ten samples; Winter Banana, one sample; Yellow Bellflower, four samples; Yellow Newtown, seven samples; and York Imperial, two samples, making a total of 117 samples embracing 24 varieties. These apples were obtained from fourteen localities in the state of Washington and also from one locality in each of the following states: New Hampshire, Indiana, Missouri, New York, and West Virginia.

Before leaving the preliminary portion of this paper the writer wishes to express his appreciation of the aid

received from those who have helped in various ways in the investigation. Thanks are due to the members of the staff of the department of horticulture for suggestions and encouragement, to the members of the library staff who have rendered aid in the study of the literature of the subject, to Mr. Geo. A. Olson, chemist of the experiment station, who has analyzed the various samples of Grimes, Jonathan, Yellow Bellflower, and Winesap, and finally to the various fruit growers and others who have cooperated in securing the fruit and have furnished notes on the conditions of production. To all these the writer takes pleasure in acknowledging his gratitude and indebtedness.

Environmental Factors

Aside from small individual differences, better called fluctuations than variations, and other more striking modifications of comparatively infrequent occurrence and obscure origin, which it is customary to explain as bud variations, if, indeed, the application of a name to a phenomenon can pass as an explanation, it is quite generally recognized that variation in any variety of fruit is due to the operation of external influences. A knowledge of the various factors which make up the environment and their influence upon plant life is necessary to an intelligent study of variation. It should be noted, however, that this influence is not necessarily the same with plants propagated vegetatively as with those grown from seed. In the latter case certain modifications of an adaptive nature which enable the plant to fit in more perfectly with its surroundings are apt to persist, while less favorable modifications tend to disappear by the elimination of the individuals possessing them. In the former case, on the other hand, the modifications observed are the direct result of the conditions, unaffected by selection, and whether desirable or not they persist as long as the environment is unchanged and the vegetative propagation is continued, unless, indeed, the environment is so unfavorable that the

changes induced are pathological in nature and the plant can not survive.

Perhaps the most important factor to which plant life is subjected is the moisture relation. This may be determined by the amount of moisture actually present or by the modifying influence of other coexistent factors which interfere with the availability of the moisture and the capacity of the plant to make use of it. Among such indirect influences may be noted the modifying effect of temperature upon the rate of absorption and transfer of moisture, the presence in the soil of certain salts or humic acids which interfere with the osmotic activity of the roots, and certain atmospheric conditions favorable to rapid transpiration. In such cases care is necessary to determine which is the direct and which the indirect cause of the modifications. If it is borne in mind that many factors cause variation through their influence on the moisture supply confusion may often be avoided.

The temperature relation is much more obscure than the moisture relation in its effect upon plant growth. Heat, being a molecular phenomenon, acts directly upon the protoplasm and its effects are therefore physiological. It is now pretty well understood that heat alone is incapable of modifying plant structure, but acts indirectly through other factors and the functions of the plant. The direct effect of temperature is limited very largely to its influence upon the rate and amount of development. A slight difference in the average temperature of the growing season influences greatly the relative development of apple varieties. The accompanying table gives the mean monthly temperature during the growing season at Geneva, N. Y., and Pullman, Wash., since the establishment of the experiment stations at those points, as well as the mean for two years at White Salmon, Wash.

Locality.	April	May	June	July	Aug.	Sept.	Oct.	Aver.
Geneva, N. Y.	44	57	67	71	69	63	50	60
Pullman, Wash.	47	52	59	66	66	58	48	57
White Salmon, Wash.	50	56	63	70	67	60	53	60

The difference in the development of certain varieties of apples at these places will be noted later. It will be seen that the season opens slightly earlier in Pullman than in Geneva and closes at about the same time. It would appear, therefore, that the better development of most varieties at the latter station is due rather to the higher temperature than to a difference in the length of season. At White Salmon the season is considerably longer than at either of the other stations, while the temperature from May to September is intermediate.

Latitude and altitude are frequently mentioned as important factors in the modification of varieties. These, however, are not primarily factors, but depend for their influence upon the effect of other factors, which in turn are influenced by the location. Differences in altitude especially result in marked changes in climate often in places geographically near together.

The light relation is of much importance to the fruit grower. It is clearly evident that the development of color in apples is largely dependent upon the sunshine, and quality also may be affected through the production of sugars. Both intensity of insolation and duration of the daylight must receive consideration. In general, tropical, arid or alpine situations are characterized by high insolation, while a long period of daylight during the summer months is a factor in northern latitudes.

The effect of atmospheric influences is largely indirect. It has already been noted that the condition of the air may modify the moisture relation through its effect upon transpiration, thus dryness, high temperature, and rarification all favor evaporation, and this effect may be increased in windy situations. Atmospheric pressure is a factor of importance in high altitudes.

The soil may be of importance as a factor in causing variation through either its chemical composition or its physical properties. The former leads to a consideration of the influence of fertilization, the latter to the effect of different methods of culture. Here again other factors,

and especially the moisture relation, have an important bearing, since one of the primary results of cultivation is the conservation of the soil moisture. There is no doubt that the nature of the soil greatly affects the crop and the matter has been given much study. The intimate association of other factors, however, makes it somewhat difficult to pick out those influences for which the nature of the soil is directly responsible.

The influence of other organisms includes not only a consideration of the effect of insect and fungus pests but in the broad sense embraces such items as pollination, pruning and thinning, intercrops, cover-crops and planting distance. Human agencies, including all operations of orchard management, might properly be included here. Many of these are, of course, indirect, exerting an influence through their effect upon some other factor.

The Law of the Optimum

Having enumerated the chief external influences to which plants are subjected during their period of development and to which variation is largely due, the question naturally occurs whether there can be formulated any basic principle or law which will express the manner in which plants react with the environment. Such a law would be of use not only in the study of variation, but would shed much light on the adaptation of plants to new environments. It would constitute a unifying principle whereby isolated facts and disconnected observations appear in proper relation and perspective. Though a discussion of this subject might logically be delayed until after the characters of the several varieties and their modifications have been noted, it is thought most fitting to introduce the statement at this point and examine the fruit in the light of such generalizations as it has been possible to make.

A plant can live and perform its functions only within certain intensities of the various factors of the environment. The degrees of intensity beyond which activity

ceases are known as the *zero points*. The plant does not necessarily die at once, but passes into a dormant state. If the intensity becomes still more unfavorable a point is finally reached at which death occurs. The minimum degree of intensity of a factor at which the plant may remain active is known as the *lower zero point*, while the greatest intensity is called the *upper zero point*. With some factors these points are wide apart, so that, other conditions being favorable, the plant will continue to develop after a fashion at any but the most extreme intensities of such factors. With other factors the limits are comparatively narrow. A plant will reach that degree of development only which is permitted by that factor which is in the least favorable degree of intensity. Such factors are called *limiting factors*. In passing from one zero point toward the other, a point is finally reached at which any given function of a plant reaches its highest state of activity. This point is known as the *absolute optimum* for that function and may not correspond to the most favorable intensity of that factor for the performance of the other functions of the plant. The point of intensity of a factor at which all the functions of the plant are performed to the best advantage is termed the *harmonic optimum*. If each factor is of an intensity corresponding to the harmonic optimum, the plant is in a condition of equilibrium known as the *ecological optimum* and will reach the highest state of activity of which it is capable.[4]

As the life of a plant is made up of various functions, so its structure is made up of a number of organs having various characters. These characters are the result of development, which in turn is dependent upon the performance of the several functions of the plant under the influence of those external conditions which make up the environment. If a factor of the environment is modified in its intensity, the balance of the functions of the plant is disturbed and the plant reacts to its changed environment by a modification of its functions which may result

[4] Schimper, A. F. W., "Plant Geography."

in a different kind of development, or in other words a variation. Having observed the close connection between the characters and the functions of the plant, we may now inquire whether the former maintain a relation to the environment similar to that maintained by the latter. Putting aside generalizations for the present and confining attention to the apple, it is to be noted that both Shaw and Stewart foreshadowed such a relationship in the papers already noted. Neither, however, carried the analysis far enough to formulate a rule of general application, though Stewart came near doing so. Shaw recognized that the highest perfection in any given variety could be attained only under the most favorable summer temperature. Stewart applied this idea to other factors than temperature in his "optimum principle," which is "that plant growth and development increase as the most distant essential factors approach the optimum." His failure to recognize the connection between the various factors of the environment, on the one hand, and the separate characters of the apple, on the other, may be accounted for by the fact that his investigations dealt only with fruit grown under slightly modified conditions, which resulted only in such slight variations that the independent modification of the separate characters escaped notice.

In examining various samples of apples produced under the influence of quite dissimilar combinations of environmental factors, the writer has many times noted the modification of certain characters more or less independently of others. It is true that characters are often found to vary together through a relationship of direct or inverse correlation. Such cases, however, are possibly as often due to the response of the various characters to the same factor of environment as to any direct connection between the characters, though the latter no doubt exists in many cases. Keeping in mind these facts and also the close relationship of function and character, the writer has formulated a principle which he believes is of general application not only to apples but to other horticultural

crops and perhaps in a degree to all plant life. For this generalization, which expresses the relationship of characters to environmental factors the name "Law of the Optimum" is proposed.

This law may be stated as follows: For any given variety there is for each character a certain intensity of each essential factor of the environment at which, other conditions remaining the same, that character reaches its highest development. When all essential factors are in a condition of optimum intensity for any character, that character will reach the most perfect development of which it is capable. A modification of the intensity of any such factor either above or below the optimum will be accompanied by a less perfect condition of the character concerned. The optimum intensity of a factor may be wide or narrow in its limits and the optimum for one character may or may not overlap the optimum for others. A variety will be at its best when grown in an environment the factors of which are as near as may be to the optimum intensity for all characters. Under such circumstances the variety is in a state of *balanced adaptation* to its environment. If removed from such an environment to one in which certain factors are distant from this state of average optimum intensity for all characters, the equilibrium is destroyed and the variety is thrown into a state of *unbalanced adaptation,* in which those characters farthest removed from their respective optima are injuriously affected, while others may be bettered by being placed in a combination of factors of an intensity nearer their optima. A discussion of the practical application of this law and its bearing upon apple culture in the northwest will be deferred for the present and taken up in a later section.

A Comparative Study of the Samples

A close study of the various lots of apples used in this experiment brings to light variations in practically all characters. Many, however, are modifications of charac-

ters inconspicuous in themselves or are slight in amount and so do not attract attention. A complete account of all variations noted would comprise a full technical description of each sample which would far exceed the limits of this paper. For this reason it is thought best to append only some brief comparative notes regarding the more conspicuous variations noted in each variety. In this connection it is well to note the origin so far as known of the varieties included in this study. Arkansas and Arkansas Black, Arkansas; Baldwin, Massachusetts; Ben Davis, probably Kentucky or Tennessee; Delicious, Iowa; Esopus, New York; Gano, probably Kentucky or Missouri; Grimes, West Virginia; Jonathan, New York; Lawver, possibly Kansas; McIntosh, Ontario, Canada; Northern Spy, New York; Rhode Island Greening, Rhode Island; Rome, Ohio; Stayman, Kansas; Tompkins King, New York; Wagener, New York; White Pearmain, probably Eastern States; Willow, Virginia; Winesap, New Jersey; Winter Banana, Indiana; Yellow Bellflower, New Jersey; Yellow Newtown, New York; York Imperial, Pennsylvania. It will be observed that all originated in the east or middle west. Most no doubt appeared as seedlings and were selected and propagated because of their excellence and value when grown under those conditions of environment which prevail at their places of origin; in other words they were individuals which happened to be in a condition of balanced adaptation to that environment. Their behavior under other environments could be determined only by actual tests, and some notes on the subject are included in the following paragraphs.

Arkansas (*Mammoth Black Twig*).—As only one sample of this variety was examined its behavior can be compared only with what is known of the variety in other localities. The fruit was more elongated and conical in shape, smaller in size and less highly colored than that produced in the warmer apple-growing sections of the east. The flesh was inferior in texture, indicating poor development. The variety seems not at all adapted to

the location where grown, but might do better at lower altitudes and in warmer situations in the state. Nevertheless, the quality is not good enough to recommend the variety for dessert, and it is to be hoped that it will not be planted extensively in the northwest. The keeping quality was excellent.

Arkansas Black.—This variety of the Winesap group attains a deeper color than the Winesap and equals that variety in size and quality. The specimens examined were not especially well colored though, it is known to color well in the irrigated valleys. It seems to be better adapted to the conditions of the state than the Arkansas. In keeping quality it was among the best.

Baldwin.—The Baldwin attains its highest perfection in New York and New England, where it is a great favorite in the markets and is produced more largely than any other variety. As grown in this state the fruit is smaller and more elongated than the eastern product and has a more deeply furrowed basin. As grown at Pullman the color lacks intensity, though the fruit is well covered. In the western part of the state the fruit is well colored, especially in the northern part of the Puget Sound Basin. The lots from White Salmon show a good many poorly colored fruits mixed with those of better color, while the quality is rather better than in those examined from other parts of the state. It is, however, inferior to the eastern-grown Baldwin and is evidently poorly adapted to the conditions of the northwest. All of the Washington-grown fruit displayed a tendency to wilt in storage and some of the lots from the western part of the state rotted seriously as a result of fungous infections not apparent on the fruit at the time of storage.

Ben Davis.—Though displaying considerable lack of balance in the adaptation of the different characters to conditions in certain parts of the state, this variety seems on the whole to reach a good degree of development in the warmer valleys. In quality the lot from Missouri was superior to those from any part of Washington, though

many of the Washington-grown apples of the variety were equal to those from most sections of the east. Striking variations in form were displayed by the fruit from different localities. Those lots from the more elevated and cooler sections of the state were of an oblong, conic form and usually had shallow irregular basins, while those from the warm valleys were less elongated and had deep and usually quite regular basins, being more like the fruit from the Ben Davis belt of the east. The fruit developed better texture and quality also in the valleys though it was coarser and more spongy than the eastern fruit. Most of the Washington grown samples of Ben Davis were more decidedly striped than those from the east. This effect is produced by the clearer yellow ground color, which in the eastern-grown fruit is more or less suffused with red. The apples from the elevated localities of Pullman, Cloverland and White Salmon were relatively small in size and poorly colored. Because of its low dessert quality, the planting of this variety for shipment to the east can not be recommended. The most desirable feature of the Ben Davis fruit is its good keeping quality. A tendency to mealiness late in the season was observed in some of the fruit from the irrigated valleys, while those grown at Pullman and Cloverland wilted badly toward the close of the season.

Delicious.—This is one of the newer varieties and when well grown is a dessert apple of fine appearance and high quality. In many of its characters, but especially in flavor and aroma, Delicious resembles the White Pearmain, though in color it bears a likeness to the Winesap group. In moderately elevated situations in some parts of the state it displays a well-balanced adaptation and attains excellent size, color, texture and quality, though none of those examined were quite equal in quality to the Delicious from New York. When grown in too low and warm a location the fruit has a tendency to become overripe and when stored tends to soften in the center, after which it loses greatly in quality. The sample from Clarkston had

a beautiful dark red color, while that from Cloverland was dull in color and poor in texture.

Esopus (*Spitzenburg*).—This is almost the only variety which the writer has examined that attains the first rank as a dessert apple in this state. In certain sections it displays a better balance of adaptation so far as flesh characters are concerned than any other variety. The samples obtained from White Salmon and the irrigated valleys were of excellent quality as dessert apples, though of scarcely as good texture as the variety attains in the east. Overgrown apples are especially coarse in texture. West of the Cascades and in the more elevated locations the Esopus does not reach as high quality as elsewhere. This variety is inclined to wilt in storage unless well grown.

Gano.—This is an apple of the Ben Davis type, but of a more uniform red color. Practically all the remarks included under Ben Davis, aside from those dealing with the distribution of color, apply equally well to the Gano. At its best, the Gano is of slightly better quality than the Ben Davis, which fact, together with its more handsome appearance, renders it a more desirable variety to plant, yet neither can be recommended in a section desirous of building up a reputation and market for dessert apples. It is interesting that both the highest color and the best as well as the poorest quality was attained by apples from the east and middle west.

Grimes (*Grimes Golden*).—This variety, like the Ben Davis, displays considerable variation in form, depending on the locality of production. The specimens from the middle west were roundish to decidedly oblate, while those grown in Washington were all more or less elongated. Those grown west of the Cascades displayed a greater tendency to a conical shape than those from the eastern part of the state, and were also poorer in quality. When grown in the more elevated sections, as at Pullman, Grimes appears poorly developed and immature and is inferior in size and quality. Those from Grandview displayed the best balance of characters and it seems prob-

able that this variety is better adapted to the irrigated valleys than to other sections of the state. All samples were more or less wilted by midwinter, except the fruit from Grandview, which remained firm but showed some tendency to rot. Scald was very bad in the latter part of the season.

Jonathan.—Although rather extensively grown in a number of localities in Washington, none of the fruit which the writer has examined gave evidence of a well-balanced adaptation to the conditions of growth which prevail in the state. All were inferior in color to the fruit obtained from the east and middle west. The apples from Clarkston and the Yakima Valley were of good size but lacked both richness of flavor and aroma. The same lack was evident in the fruit from the western part of the state. At Pullman a pretty good quality is attained, but the fruit does not come up to the requirements as to size and gives other evidence of imperfect development. At Cloverland and in other elevated locations fruit of a poor texture and deficient coloring is produced. Jonathan seems to reach its highest development in certain sections tributary to the Ohio valley and the Washington-grown Jonathans can not compete with fruit from that section when well grown. The samples from Morgantown, West Virginia, were of a beautiful clear dark red color, good size, fine tender flesh, and very high quality. In storage these specimens remained firm and retained their flavor until April. The others wilted considerably after midwinter.

Lawver.—This variety attains good size and fine color in the irrigated valleys, but the quality is not good enough to recommend it to the fruit growers of the northwest. The variety ordinarily keeps well but the specimens stored proved to have poor keeping quality—owing to fungous infection.

McIntosh.—The McIntosh is deserving of attention as a variety of high quality which appears to have a fairly well-balanced adaptation to certain sections of the north-

west. At Pullman the elevation is too great for the best development of the variety, but the Spokane Valley produces McIntoshes of a high degree of excellence. There is good reason to believe that the valley of the northern and northeastern sections of the state can rival the Bitter Root valley of Montana in the production of this variety. The fruit stored wilted badly by midwinter and lost much of its flavor soon after.

Northern Spy.—Of all the varieties examined the Northern Spy seems least adapted to the conditions of growth in this state. As produced in New York and New England this fruit is a dessert apple of the highest quality when well grown and properly colored. In Washington east of the Cascades the color fails to develop and the quality is much inferior to that of the eastern-grown fruit. In the western part of the state the color develops as well as in the eastern states, but the quality is no better than elsewhere in the state. The unsurpassed cooking quality of this variety seems to be largely retained, however, which is its only redeeming feature. It may be worth planting to a limited extent as a culinary fruit for home use, but can not compete in the markets with the eastern-grown Northern Spys. The specimens from the western part of the state were largely infected with fungi, resulting in much decay early in the season. Those from Pullman and Clarkston kept fairly well, though the former wilted badly late in the season.

Rhode Island Greening.—This variety, together with Baldwin and Northern Spy, constitutes the most prominent and successful apples in the orchards of New York and New England. They are also among the varieties least adapted to the conditions found in this state. Their perfect balance of adaptation to eastern conditions is probably to a large degree responsible for their popularity in the east and may also account for the lack of balance which they display in the northwest. As grown at White Salmon and at Pullman the Greening reached a good size, but was decidedly inferior in quality to the specimens

from New Hampshire. At Pullman the fruit was rather flat and strongly ribbed, while at White Salmon the apples were oblong in shape and had, as a rule, rather small cavities. It can not be recommended for Washington, except possibly for local use as a culinary fruit. This variety is a fairly good keeper. Those grown at Pullman wilted badly late in the season, while the lot from White Salmon gave evidence of considerable fungus infection.

Rome (*Rome Beauty*).—This is one of the most popular varieties grown in the state east of the Cascade Mountains and is about the only commercial variety which reaches good marketable size in the high uplands of the Inland Empire. The Rome reaches its highest development in the Jonathan belt of the middle west. The best specimens examined, all characters considered, came from Morgantown, West Virginia. They were of a nearly uniform deep red color, of good size and attractive form, and of pretty good quality for the variety. In many parts of Washington the Rome fails to color well. The specimens from White Salmon and Grandview were especially poor in color. The latter were overgrown and of poor quality, while the former were among the best of the variety. The usual form of the variety is round or nearly so, varying to somewhat roundish conic or roundish ovate. The form of the cavity is subject to quite a little variation. As produced at Pullman and other elevated sections of the state the cavity is very shallow, but becomes deeper in the valleys. The specimens from West Virginia had fairly deep cavities. Indeed it seems probable that those localities which produce Ben Davis of the elongated type also produce Romes with the shallow cavities. The Rome is by nature a culinary apple. In quality it is but little better than Ben Davis. It seems unfortunate, therefore, for the lasting reputation of the industry, that it should have become so firmly established in northwestern horticulture. It is to be earnestly hoped that it may in time be replaced by a variety of better quality. In its adaptations to the conditions of the state, the Rome seems to be fairly well

balanced in most of its characters. The balance, however, is not the same in all sections and is nowhere quite so perfect as in certain localities in the middle states. Most samples kept well until the latter part of the season and then became mealy. The overgrown specimens from Grandview were the first to break down in this way. Those grown at a greater elevation showed a slight tendency to wilt late in the season. None of the samples displayed an inclination to rot until late in the season.

Stayman Winesap.—In both size and quality the Stayman is the best of the Winesap group. Its most serious fault is a rather dull color which often fails to cover the fruit well. The samples obtained from the middle west were of better color and texture than those grown in Washington, though the lot from Indiana were very coarse in texture. Those grown at Pullman were small and inferior in every way. The fruit from Grandview was especially large, flat, and fairly well colored, while that from White Salmon was more elongated, slightly less colored, and rather more aromatic in flavor. These two lots retained their firmness in storage much longer than the others and those from White Salmon scalded badly late in the season. It is very similar to the Winesap in its adaptations.

Tompkins King.—This variety is popular in the western part of the state, where it attains a large size and good color, though the latter character develops well at Pullman. None of the samples equaled in quality the variety as grown in New York. Those grown at Pullman had a very good flavor, though the flesh characters were those of poorly matured fruit. The fruit from the western part of the state was of a fairly elongated conic form, while that grown at Pullman was shorter and strongly ribbed. This variety appears to be but poorly adapted to Washington conditions. The fruit grown at Pullman wilted badly late in the season, while that from western Washington rotted considerably owing to fungus infections.

Wagener.—Though of the Northern Spy class, the

Wagener displays a much better balance of adaptation to the conditions of the state than the Northern Spy. It seems to reach its best development in the cooler regions of the state. The specimens from Grandview were of good size and very juicy, but were poor in color, coarse in texture, and deficient in flavor. Wagener develops especially well in the Spokane Valley. The specimens from Opportunity were large, well colored, and of excellent quality, though somewhat coarse in texture. Those grown at Pullman were more aromatic but possibly not so rich in flavor and did not develop sufficient size. This variety does well west of the Cascades and especially in the northern part of the Puget Sound Basin. The specimens from Eastsound were large, highly colored, and fine in texture, but less aromatic than the eastern Washington fruit. The samples obtained from West Virginia gave evidence of having been grown too far south. They were poorly colored and of rather poor texture, but of good size and excellent flavor. In form the fruit from Opportunity was roundish, that from Eastsound roundish conic, while the remainder was decidedly flattened and all samples were more or less strongly ribbed. This variety shows very little tendency to wilt in storage. The fruit from the highlands keeps well, but that from the irrigated valleys shows a tendency to physiological decay. Scald is serious after midwinter.

White Pearmain (*White Winter Pearmain*).—In general appearance this variety often closely resembles the Yellow Newtown, but is usually more elongated and more largely blushed. Moreover, it is quite different in flavor and is remarkable for its fine aroma. It is a variety of high quality and attractive for a yellow apple, moreover, it attains its good qualities in the irrigated valleys better than on the highlands, the specimens from Cloverland being dull and green in color and poor in texture, but well blushed and highly aromatic. Its worst fault is susceptibility to the apple scab. It would seem to be better adapted to growing in the state than some of the more

popular varieties. The fruit from the Yakima Valley retained its firmness much better than that from Cloverland, but lost somewhat in flavor toward the close of the season.

Willow (*Willow Twig*).—The writer has examined this variety only as grown in the elevated portions of eastern Washington. In such locations it does not develop especially well in either size or color and is of too poor quality to be worthy of consideration. Moreover, it wilts badly in storage, though when well grown the fruit has excellent keeping quality. It is evidently poorly adapted to this section.

Winesap.—In some of the irrigated valleys this variety is one of the most popular apples grown. It attains a good marketable size and an attractive color, though none of the samples examined were equal in color or quality to the Winesaps from Indiana and West Virginia. In elevated localities, as at Pullman, Cloverland and White Salmon, the fruit is small and poorly colored and has flesh characters indicating imperfect development and maturity. As grown in the irrigated valleys the fruit is apt to be deficient in flavor, and, if large, coarse in texture. The lot from Cashmere showed the best balance of characters of any Washington, grown specimens, but these were in no way superior to the Winesaps from West Virginia. It is probable that the better grown fruit from the eastern Winesap districts is equal to that grown in Washington in all respects, with the possible exception of size, which, if large, is, as noted, apt to be accompanied by deterioration in quality. It is evident then, that the balance of adaptation of this variety to northwestern conditions is imperfect at best and that the planting of Winesaps in Washington may easily be overdone. This variety proved to be one of the best in keeping quality. Those from Pullman and Cloverland wilted late in the season, though most of the other lots were in excellent condition in April and a few were held in storage until July.

Winter Banana.—As only a single lot of this variety

was examined in detail, it is difficult to make very positive statements regarding its behavior in the state. Though less desirable than a red apple, it is a variety of handsome appearance and is fairly good in quality. It is perhaps rather better adapted than the average to certain sections of the state and appears to develop best in fairly elevated situations. It is especially well liked in the Spokane Valley, and fruit grown there is said to have good keeping quality, though the specimens from western Washington were past season by midwinter. They wilted badly and showed much scald.

Yellow Bellflower.—This variety appears to be better adapted to the western part of the state than to the irrigated valleys. The apples from Clarkston were coarser in texture, milder in flavor and poorer in quality than the samples received from the east. There were no very striking differences in form, structure or appearance except that the eastern Bellflowers were more often blushed than those from Clarkston. The apples from Puyallup were overgrown specimens from young trees, were coarse and spongy in texture, and inferior in quality. As this is a tender fruit, easily injured by careless handling, and does not appear to be especially well balanced in its adaptations, it is not desirable to plant extensively for shipping. Moreover, it is not a good keeper. The specimens from Puyallup were practically past season when received and those obtained from the east were more or less injured and such specimens decayed quickly. Some of the lot from Clarkston, however, kept sound and firm until past midwinter, but deteriorated in flavor toward the last.

Yellow Newtown.—When at its best, this variety has few equals. It is narrow in the limits of its adaptations and its successful culture in the eastern states is confined to small areas, where, however, it is in nearly perfect equilibrium with its environment. In many places in the northwest it is grown successfully, though it scarcely equals in quality the best eastern product. The fruit from White Salmon and some of the irrigated districts

was of excellent quality, but coarser and less delicate in texture and of not quite so good flavor as the apples from West Virginia. The specimens from Cloverland were hard and green and gave evidence of imperfect maturity. Evidently the elevation is too great for its proper development. The single sample from western Washington consisted of well-colored, extensively blushed fruit, but was inferior in quality. Owing to its limited area of successful production in the east, it is worth planting in Washington wherever its characters give evidence of a fair degree of balance of adaptation with the environment. This variety is perhaps a better keeper than Winesap. Some of the fruit from White Salmon kept in good condition until July, though overgrown fruit and that which has been exposed to heat before storage showed signs of physiological decay late in the season. Underdeveloped specimens wilted in storage.

York Imperial.—In sections of Virginia and neighboring states the York Imperial occupies the place of supremacy held by the Baldwin farther north. This is doubtless due to its perfect balance with the environmental conditions of that region, and, like the Baldwin and other sorts perfectly adapted to their eastern habitat, this variety finds itself out of equilibrium when moved to the northwest. The apples from western Washington were of good size and color, but were coarse and undesirable in texture and poor in quality. The specimens grown at Pullman were smaller, more elongated, and less compressed than the others, and the axes were less oblique. They were somewhat better in quality, though not good enough to justify more extensive planting. The fruit wilted in storage, and that from western Washington gave evidence of fungous infection and scalded badly after midwinter.

Discussion of the Effect of Environment Upon Apple Characters

Size.—Size is the direct result of development. An apple will reach its maximum in growth when all factors

are at the variety optimum for the physiological processes upon which development depends. A departure from this optimum, whether toward a greater or less intensity, means a decrease in size, as is observed in approaching either the northern or southern range of a variety. It has been frequently noted, however, that the optimum for growth is not the best combination of factors for the development of certain other desirable characters, so that it is well to choose an environment having certain factors in a somewhat less degree of intensity, being content with fruit of fair size but superior in other respects. Since the apple contains about 85 per cent. of moisture it is evident that the water supply is a factor of prime importance in determining size. It is possible by excessive irrigation to force an abnormal growth of the fruit, though always apparently at the expense of texture, flavor, and keeping quality. It is evident, then, that if fruit of good quality is expected, irrigation must be moderate in amount, especially with vigorous young trees. Thinning may result in increased size owing to the larger amount of moisture available for each fruit. Temperature and length of season are of importance in determining, respectively, the rapidity of growth and degree of development attained.

Form.—One of the striking features revealed by the study of a number of varieties from several localities is the fact that the modification in shape due to the difference in environment is by no means uniform for the several varieties. Some varieties are quite constant in shape while others are much more plastic in this respect. Moreover, certain varieties are much more easily influenced than others which respond in the same way, while still others respond differently to the same factors. One of the most frequently observed and conspicuous modifications of form consists of the elongation of the axis of the fruit relative to the horizontal diameter. This character has been especially studied, in the case of the Ben Davis, by Shaw, who found the elongation most noticeable in fruit from the northeastern states, the mari-

time provinces of Canada, and the Pacific coast. Shaw's papers dealing with this subject have already been noted. Upon studying the climate in these localities, it was found that the temperature for two or three weeks after the blooming season was notably lower than in the sections where the Ben Davis assumes its normal shape. Since this appeared to be the only factor constant for the several localities, it is suggested as the explanation of this variation. It has been shown, however, that temperature is incapable of influencing form except by its action through the functions of the plant in modifying the effect of some other factor. It is the writer's opinion that the elongation is due to the relative moisture supply of the different parts of the apple at this period of development as influenced by the temperature; that it is primarily a modification due to the moisture relation rather than to the direct effect of temperature, the latter being a secondary cause. The rapidity of circulation of the sap and therefore the supply of moisture to the organs of the plant is greatly influenced by the temperature. It is a well-known fact of plant physiology that much less moisture passes through the plant in the cool days of spring than during the warmer weather of midsummer. A reduction of the temperature at this time results in a still more sluggish movement of the sap. In the period immediately after blooming the energy of the plant, so far as the development of the fruit is concerned, is directed primarily to the proper nourishment of the growing seeds and the adjacent parts. If at this time the circulation of the sap is retarded by a temperature unwontedly low for the variety, the moisture supply of the fruit is lessened and a relatively larger amount goes to the seeds and adjacent parts, while the pulpy portion of the fruit receives a more scant supply. As a result, the axillary development is proportionately greater than the swelling of the fruit due to the accumulation of moisture in the superficial tissues. After some two or three weeks the form of the fruit becomes fixed and is not noticably influenced by the moisture supply thereafter.

The elongation of the fruit is usually accompanied by a constriction of the apex resulting in a conical form. This may be due to the greater development of the basal portion, which is adjacent to the point where the sap enters the fruit and may therefore be better supplied, though the physiology of fruit development is in need of further study. In the Grimes, however, an oblong form results. The McIntosh, as grown at Pullman, is often decidedly obovate, a variation which the writer ascribes to the same influences that produce the elongated conic form of the Ben Davis and other varieties, though in this variety the response is somewhat different. The Rhode Island Greening, Willow and Wagener, as a rule, fail to assume an elongated form in localities where it is well marked in some other varieties. Also in certain varieties which are naturally conic in form and considerably elongated, as Delicious and Yellow Bellflower, this effect is not evident. The larger number of varieties, when grown in this state, have a more ribbed form than the same varieties in the east. This seems to be due to a lack of balance in adaptation, though the particular factor which gives rise to the variation has not been determined. Some varieties, like the York Imperial and the Yellow Newtown, are compressed in form, that is elliptical in section, and have an oblique axis when grown in certain environments. These characters seem to be in some way related to the better development of the fruit, as they are less evident in fruit from the elevated and unfavorable sections of the state. Beach has noted in the "Apples of New York" a similar difference between the Newtowns of western New York and those of the Hudson Valley, the latter having a more oblique axis and elliptical form.

Stem.—The stem is one of the most variable structures of the apple, and, owing to the fact that stems of different lengths, diameters and shapes are commonly found in any lot of apples grown under practically uniform conditions, it is difficult to associate such variations with the environment. The writer has noted, however, in the case of some short-stemmed varieties, like the York Imperial,

that those lots grown under less favorable conditions had, on the average, longer stems than others grown under a more favorable environment.

Cavity.—The most conspicuous variation in the cavity is in its depth. This is of especial note in the Rome, which has a very shallow cavity in most parts of the state. This is doubtless due to the same cause which produces the elongated form of the fruit in many varieties, namely the elongation of the axis resulting from a deficient moisture supply incident to a low temperature after the blooming season. In this variety the elongated axis obliterates the cavity instead of modifying the general outline of the fruit. The same variation is also noted to a less degree in a number of other varieties. An especially furrowed cavity is often observed associated as a rule with the ribbed form of fruit.

Calyx.—The writer has failed to observe any modifications of importance in the calyx lobes of the fruit. The size of the calyx cup or "eye" of the apple is influenced by the development of the fruit. In large fruit this opening is apt to be large, so that the lobes are separated, resulting in an open or partly open calyx. Small or poorly developed apples, on the other hand, usually have the calyx closed.

Basin.—The depth of the basin seems to depend upon the same factors as that of the cavity and seems to be much more readily influenced than the latter. The width is often associated with the form of the apple, a very constricted apex resulting in a narrow basin. A much furrowed basin results from a combination of factors unfavorable to the best development of the fruit.

Skin.—Statements have often appeared in regard to the effect of various climatic factors upon the thickness and toughness of the skin. Estimates of these characters, however, appear to be based entirely upon sense impressions of the observers, although it would seem that exact measurements would not be especially difficult. In the absence of such accurate data, an expression of opinion

would be premature. Dry air and sunshine are favorable to the production of clear, smooth skin.

Color.—There seems to be no doubt that the coloration of apples depends upon the influence of several factors of which light is usually the most important. The importance of light is easily demonstrated by covering the fruit during development either wholly or in part. The intensity of illumination is also, evidently, quite narrow in its limits, so that a point is soon reached at which the color begins to pale owing to excess of illumination. It has been frequently noted that apples grown near the southern limit of the range of a variety are paler than those grown farther to the north. This effect appears to be the result of an excess of the two factors, heat and light. It has been mentioned in the discussion of the characters of several varieties that, contrary to the general impression, those grown in Washington east of the Cascades where insolation is intense were less highly colored than those from western Washington or the eastern states. The most marked example of this kind which the writer has observed is the Northern Spy. Again, contrary to the general impression, most of the samples from elevated locations were poorly colored, a fact which may be attributed partly to the strong insolation and partly to the poor development due to the low summer temperature. It appears, therefore, that either too strong or too weak illumination may result in poorly colored fruit and that the best color is developed under a condition of optimum intensity of the light.

It is suggested above that temperature may influence color. This is most commonly observed in the case of apples grown under conditions of too high summer temperature, though a deterioration in color also results if the temperature is much below the optimum for the variety. It is often stated that apples become more highly colored the farther north they are grown. This is only true in part. Those varieties which are adapted to the most northerly portions of the apple belt are able to develop their highest

color at the limit of winter hardiness of the tree. The southern varieties, on the other hand, require for the best development of color a higher summer temperature than is experienced in the northern localities. The Winesap, for example, when grown in Central New York is partly covered with a pale red. At Pullman the majority of varieties color poorly, due at least in part to the cool climate. That the temperature and not the shortness of the season is the factor involved is shown by the fact that most of these varieties color well in central New York which has a season of about the same length though averaging several degrees warmer.

Cultural conditions may influence the color to a certain degree. In general those processes of orchard management which favor the early maturity of the fruit result in improved color, especially in localities having a short growing season. Pruning and wide planting are regarded as favoring high coloration by admitting light into the tree, though it is possible that in regions where the light is intense these factors may not be of so great importance in their effect upon color as in less sunny locations. Something has been said of the influence of the soil in the discussion of the literature and it has been noted also that studies of the effect of fertilizers upon the color have not yielded satisfactory or uniform results. The influence of iron compounds is worthy of brief discussion in this connection. It seems evident, from the chemical studies which have been made, that the red pigment includes iron in its composition. This has sometimes been assumed to mean that the chief requirement for highly colored fruit is the presence of plenty of available iron compounds in the soil. As a matter of fact, iron is also necessary to the formation of chlorophyll and most soils contain an abundance of that element for the purpose. From the chemical data compiled by Stewart[5] it appears that the ash of the fruit contains a much smaller proportion of iron than that of the leaves. It is logical to conclude, therefore, that soils containing suffi-

[5] Pa. Sta. Rept. for 1910–11.

cient iron for the development of chlorophyll in the leaves are also fully supplied for the formation of the red pigment of the apple.

Internal Structure.—The form and relative development of the core and associated structures are subject to numerous variations, which, however, are seldom so conspicuous as to attract attention unless closely studied, and appear to be of little practical importance to either the grower or consumer of the fruit. The number of seeds may be mentioned as an indication of the thoroughness of cross pollination and in most varieties the presence of one or more well developed seeds is a requisite to the proper development of the fruit. Small or poorly developed fruit, the result of too short a season or too low a temperature, is apt to have the core closed and axile, or nearly so, while in the same varieties good development is usually associated with a more open abaxile core. The carpels of such poorly developed fruit are usually entire and smooth, while those of the better-grown fruit are more or less cleft and often tufted.

Flesh Characters.—From the standpoint of the consumer, these are by all odds the most important characters of the fruit, though lost sight of through the emphasis placed on external characters, and no grower who has at heart the permanent prosperity, extension and normal development of the industry can afford to look upon quality as a secondary consideration. Neglect in this matter is sure to result sooner or later in a bad reputation for the fruit among a considerable proportion of buyers, which appearance and advertising will not be competent to overcome. The fact can not be denied that the great majority of varieties fail to attain as high quality in the northwest as when grown in the eastern or middle states where nearly all of them originated, while at the same time they may excel in other important characters. This is especially true of most of the choice dessert apples. Such unequal development can have no other interpretation than that these varieties are in a state of unbalanced adaptation to the environment. This

fact being recognized, the main question is, How can this disadvantage be overcome? Evidently the solution does not consist in a steadfast refusal to face the situation and vehement declaration that the fruit of any particular district is the best that can be produced. Such tactics, though well meant, can be permanently successful only when the statements are justified by the facts. If apple culture in Washington is to be maintained upon a sound basis it will be necessary first of all that growers shall exercise great care in planting to choose those varieties most nearly in equilibrium with the environment in the various sections of the state, at the same time avoiding over-irrigation or other errors in orchard management which may tend to an unequal development of the characters of the fruit, usually at the expense of quality. Even this, however, may be but a temporary makeshift, since few if any of the better varieties possess the requisite power of adaptation. It will be necessary first of all to determine if the variations which appear when apples are grown from seed in the northwest are more favorable in character than those which are displayed by introduced varieties. If such should prove to be the case the writer is under the conviction that the apple culture of the northwest should ultimately be largely made over on a basis of new varieties of local origin. A number of such varieties have already appeared, but unfortunately some of them have been chosen with little regard for quality. No work of greater value to the future horticulture of the region can be undertaken by the experiment stations of the northwestern states than the development of apple varieties of high quality and perfect adaptation to the various sections of their respective states.

The apples of high quality which show a fair degree of adaptation to the irrigated sections are Esopus, Yellow Newtown, Delicious and White Pearmain. The last was found by Lewis, of the Oregon station, to be one of the best pollenizers on every variety tested. Jonathan, Winesap and Stayman, though largely grown, shows in general a poorer balance of characters. In the more

elevated valleys Wagener, Delicious and McIntosh are doubtless most worthy of culture. The highlands of eastern Washington are very poorly adapted to the growing of winter apples, though some of the early apples do fairly well, among which may be mentioned Oldenburg, Gravenstein and Yellow Transparent. On account of the abundance of sunshine the Oldenburg develops a high sugar content for the variety which counteracts its natural acidity and results in an apple of pretty good dessert quality. Of the winter apples, Rome reaches good marketable size but the quality is not high and the eastern market should not be jeopardized by shipping this variety. The Palouse, an apple of local origin, is of much better quality, but has little standing in the market as yet. The Dutch Migonne, a variety from western Europe, shows a better balance of characters in eastern Washington than in most other sections of this country. It is of good size, fairly well colored and excellent in quality.

Many varieties popular in the eastern states color better west of the Cascades than in eastern Washington, though there is usually manifest a lack of balance in other characters. In certain respects the environment resembles that of western Europe and many of the varieties of cherries, plums, prunes, and other fruits of that country do very well here and, indeed, in other sections of the state as well, though in a number of instances varieties of northwestern origin are gaining in favor rapidly. Apple breeding, however, requires more time for its accomplishment and further importations of fruits, especially apples, adapted to the mild climate of western Europe would no doubt prove an advantage through the possible discovery of sorts adapted especially to the western part of the state.

Quality is not in itself a simple character. It depends upon all the characters of the flesh which determine the desirability of the fruit for eating, such as texture, juiciness, aroma and flavor. Fineness of texture evidently depends upon a proper combination of favorable factors.

Conditions favoring rank growth result in coarse texture, as was observed in several instances in the case of apples grown under irrigation, especially if the fruit was overgrown. Some of the fruit from young trees also was overgrown and coarse. Tenderness depends upon the development. Poorly grown, under-developed fruit grown where the temperature is too low or the season too short for the variety has hard flesh which becomes spongy rather than mellow toward the end of the storage season. Overgrown fruit of certain varieties, on the other hand, often shows lack of coherence between the cells, often accompanied apparently by larger intercellular spaces, and such fruit tends to become mealy as the season progresses. Juiciness is primarily a manifestation of the amount of moisture in the fruit, but is also associated with the tenderness of the cell walls and their tendency to break rather than to separate. In general an abundance of moisture results in juicy fruit though the juiciness is not in proportion to the moisture supply. The substances which give the apple its aroma are present in such small amounts that their investigation is difficult. They are volatile compounds and affect the flavor of the apple largely by their action on the sense of smell. A cool climate is favorable to their production and it was often observed that they were most strongly developed in the apples from elevated situations. Flavor depends upon the kinds, amounts and relative proportions of the soluble solids, especially the balance between sugars and acids, and will be given further consideration in the discussion of the chemical composition. Immature and under-developed apples contain some tannic acid, which is often sufficient in amount to give an astringent character to the fruit.

Keeping Quality.—In its relation to the environment, keeping quality evidently follows the same rule as other variable characters of the apple, namely, that for any variety the keeping quality depends upon the optimum intensity of the various external factors. Apples grown where the temperature is too low or the season too short

to develop the fruit to a proper stage to keep well, soon wilt, lose flavor and scald, or show other evidence of deterioration as was frequently observed in the fruit from high altitudes. On the other hand, too great excess of certain factors results in overgrown or overripe fruit having a tendency to rot, mealiness, or physiological decay, as in the case of the Yellow Bellflowers from Puyallup and some of the fruit from the warm valleys. The balance of factors favorable to good keeping quality does not appear to differ much from that which produces the fruit which is most desirable in other characters, though it is possible that the required intensity of some factors may be slightly lower. It appears, therefore, that a good balance of the other characters of the fruit and perfect adaptation to the environment will be accompanied, as a rule, by good keeping quality, provided that the fruit is properly handled and not infected with disease, while an unbalanced adaptation of characters to environment is likely to result in poor keeping quality. It seems probable that irrigation in itself does not result in poor keeping except when improperly applied or carried to excess or associated with other factors in such a way as to destroy the equilibrium of the environment. The relation of specific gravity to the keeping quality is discussed in a succeeding paragraph.

Specific Gravity.—It has long been understood that varieties of apples differ in their relative weights; thus Wolf River is comparatively light and Baldwin is generally regarded as a heavy apple. The only record found of the determination of specific gravity of apples is that of Howard's work in the National Bureau of Chemistry, Bulletin 94, in which it is noted that the specific gravity diminished 3 per cent. to 5 per cent. during storage. From the account it is not clear whether the determinations at the different dates were made with the same apples. The decrease of specific gravity is ascribed to the increase of air spaces between the cells due to the softening of the middle lamella. In the specific gravity determinations made by the writer a number of points was noted.

The different lots of a variety may differ considerably in specific gravity, though as a rule running somewhat close together, thus Ben Davis and Gano are apples of low specific gravity, while Grimes, Stayman, Wagener, and Yellow Newtown run rather high and Baldwin and Rome may be classed as medium in this respect. Overgrown apples were low in specific gravity, probably owing to more air space between the cells. This is more apparent upon examining the results for individual apples than upon comparing the average for different lots, as in the latter case the extremes are modified by averaging with the results for more normal specimens. On the other hand, small and rather undeveloped apples are apt to have a high specific gravity on account of their solid flesh and usually closed core. Juicy apples, if not overgrown, have a high specific gravity when the juiciness is due to a high moisture content.

The relation of specific gravity to keeping quality is of interest. While some late keeping varieties have normally a low specific gravity, those lots of a given variety having a high specific gravity for the variety are usually the best keepers. This is in line with the fact that certain causes which give rise to fruit of poor keeping quality also produce a low specific gravity. This is shown very strikingly by a comparison of the specific gravities as calculated month by month through the season. As the calculations were made at the time the fruit was found fit for use, the monthly averages show the steady increase in specific gravity with the better keeping quality of the fruit, though modified somewhat by the peculiarities of the different varieties which happened to be in season at different times. These averages are as follows: November and December, 0.787; January, 0.787; February, 0.810; March, 0.831; April, 0.852. Though these results may seem to be at variance with Howard's observations it is possible that if the same specimens had been tested at intervals a decrease in specific gravity would have been noted.

Chemical Composition.—In order to throw some light,

if possible, upon the relation of chemical composition to the other characters of the apple and to determine whether the composition is influenced by the environment, the juice of the various samples of Grimes, Jonathan, Winesap and Yellow Bellflower was analyzed by the department of chemistry.

The juice of the Grimes and Winesap contains, as a rule, a decidedly higher percentage of total solids than that of the Jonathan and Yellow Bellflower. It is also generally higher in specific gravity and has a greater viscosity. In Grimes and Yellow Bellflower the juice of the eastern-grown fruit contains a large proportion of total solids than that of the Washington grown fruit, though this rule does not hold good in the other varieties. The apples from the irrigated valleys and western Washington were low in total solids with the single exception of the Winesaps from Cashmere. The analyses fail to show any constant difference in sugar content in favor of the fruit produced in the sunny climate with long hours of daylight characteristic of the apple-growing sections of the state.

In Grimes the total sugars are fairly high and the proportion of sucrose is especially large. The acid content, on the other hand, is low as a rule. The result is a rich, mild or nearly sweet flavor. A sample from Puyallup showed the lowest sucrose content combined with the highest acid content, and this was the least rich as well as the most acid in flavor.

Jonathan, on the other hand, displays a low content of total sugars and especially sucrose, while the acid content is slightly higher than in Grimes, indicating a subacid apple, lacking in richness. The lots from Missouri and Indiana were highest in sucrose but were of scarcely as good quality as the Jonathans from West Virginia. The latter were low in both sucrose and acid, but displayed a good balance between these constituents, indicating an apple with rather thin juice, not very rich, but pleasant and refreshing. Its evident superiority resulted largely

from the fine texture and well-developed flavoring constituents not shown by the analysis.

The Winesaps, though high in total sugars, are low in sucrose, indicating a heavy juice rather lacking in richness. The comparatively high acid content corresponds to the sprightly subacid character of the fruit. The highest acid content was found in the fruit from Cloverland, where it is associated with a total lack of sucrose resulting in a comparatively poor fruit. The apples from Cashmere and White Salmon were also devoid of sucrose in the juice, but the acid content was low and the flavoring principles well developed, as a result of which the quality was fairly good. The poorly developed Winesaps grown at Pullman were deficient in sucrose, acid, and flavors and were correspondingly poor in quality.

The Yellow Bellflowers, though low in total sugars, were rather high in sucrose and also in acid. The balance between these constituents is good and results in a moderately rich, pleasant, subacid flavor.

Summary

The opportunity for the study of apple variation was unusually good, owing to the facilities afforded for the examination of fruit from various localities and different environments, and it has been possible to work out the fundamental principle upon which variation resulting from external factors depends and to apply it in the study of environmental adaptations. This principle, the *Law of the Optimum,* states that, for any given variety there is for each character a certain intensity of each essential factor of the environment at which, other conditions remaining the same, that character reaches its highest development.

In the application of this law to varietal adaptations, the essential point is the proper balance between characters and environmental factors, that is, all factors should be of such an intensity as to permit a good all-round development of the fruit. In the absence of such

a balance certain characters may fail to reach a proper degree of development while others develop to excess.

The failure in quality and other respects of many of the best dessert varieties of apples when grown in Washington is due to such a lack of balance. Practically all of them originated under a much different environment and were selected and came into prominence owing to their perfect balance of adaptation in localities having a set of external conditions similar to those under which they originated. The hope of northwestern apple culture in the future lies in the careful selection of varieties and the origination locally of varieties of high quality showing adaptation to the conditions of growth in the various sections. In the meantime plantings should be made from those varieties of high quality which show the best adaptation. These are Esopus, Yellow Newtown, White Pearmain and Delicious for the irrigated valleys, and Wagener, Delicious and McIntosh for the higher valleys of northern and eastern Washington. Jonathan, Stayman and Winesap show a poorer balance and should not be planted too recklessly. The climate of the Pacific coast resembles that of western Europe more than that of the eastern states, and further importations of European varieties is desirable especially for testing west of the Cascades.

The moisture relation is probably the most important factor in inducing variations, and is doubtless responsible for certain variations which have been ascribed to other causes which act indirectly by modifying the moisture supply. The elongation of the fruit following a cool period after blooming may result from a diminished circulation of the sap, giving rise to an insufficient supply to provide for the simultaneous development of the fleshy portion and elongation of the axis. Variation in the depth of the cavity and basin in certain varieties is probably to be explained in a similar way.

Color modifications depend to a great extent upon the light relation and somewhat upon development as influenced by temperature. The optimum intensity for the

production of red pigment is quite narrow in most varieties and poor color may result from either deficiency or excess. Latitude and altitude affect the color only as they modify the factors upon which color depends, causing them to approach or recede from the optimum. The influence of elements in the soil is not well understood. It is probable that soils containing sufficient iron for the proper development of chlorophyll contain an abundance for the production of red pigment in apples.

Aside from such differences as depend upon the handling of the fruit, variations in keeping quality appear to follow the law of the optimum in the same manner as the other characters of the fruit. Conditions which favor the best all-round development result, as a rule, in good keeping quality. Apples grown under irrigation are said to keep poorly probably because of their unbalanced adaptation to the environment. Certain factors which favor development and maturity are present in excess, resulting in overgrown or overripe fruit.

Varieties differ in specific gravity according to the extent of intercellular spaces in the flesh and the openness of the core. Overgrown specimens are low in specific gravity. As a rule, those lots which kept best in any variety had the highest specific gravity.

Chemical composition is associated somewhat with quality. High sucrose content results in richness of flavor. Fruit of high quality has the sugars and acids well balanced and the flavoring constituents well developed. A heavy juice is usually associated with a high content of soluble solids. Fruit grown under irrigation is ordinarily rather low in soluble solids. There seems to be no constant relation between the amount of sunlight and the production of sugars, and flavors appear to develop best in a relatively cool climate.

VARIATION AND CORRELATION IN THE MEAN AGE AT MARRIAGE OF MEN AND WOMEN

SOMEWHERE in sociological literature we have met with the statement that whereas the mean age at marriage of men differs from district to district because of social and economic conditions, the mean age at marriage of women varies but little because of these factors. In view of the high "assortative mating" coefficient[1] for age of bride and groom, this statement seemed so remarkable as to be open to question.

Its validity can be very easily tested provided the mean age at marriage of men and women from a series of districts differing in economic and social conditions are available. If the mean age of women is independent of these conditions, or far less dependent upon them than that of men, one should find (i) that the variation of mean age of brides is lower than that of mean age of grooms, and (ii) that for a series of districts the coeffiicent of correlation between the mean age of brides and grooms is very low.

The only suitable series of data that we have been able to find is that given by A. Dumont[2] for the average age in years and months at first marriage of the males and females of the 87 departments of France. Grouping his data in classes of five months' range, we find, in terms of months:[3]

	For Men	For Women
Mean	$337.76 \pm .80$	284.43 ± 1.03
Standard deviation[4]	$11.03 \pm .56$	$14.25 \pm .73$
Coefficient of variation	$3.26 \pm .17$	$5.01 \pm .26$

[1] See Lutz, *Science*, N. S., Vol. 22, pp. 249–250, 1905. For a general review of the literature of assortative mating see Harris, *Pop. Sci. Mo.*, Vol. 80, pp. 476–492, 1912.

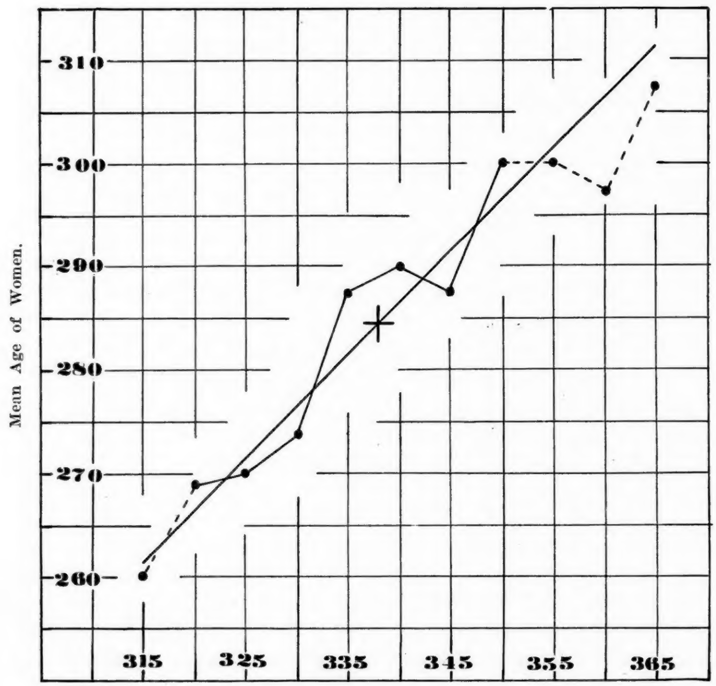
[2] Dumont, A., *Rev. Ecole Anthrop. Paris*, Vol. 14, p. 163, 1904.

[3] The results given by the ungrouped data are:

	For Men	For Women
Mean	$337.87 \pm .83$	284.45 ± 1.01
Standard deviation	$11.49 \pm .59$	$14.00 \pm .72$
Coefficient of variation	$3.40 \pm .17$	$4.92 \pm .25$

Considering the shortness of the series, the results are in as good agreement as could be expected.

[4] Without Sheppard's correction for the second moment.



Mean Age of Men.

We note that the women marry on an average about four years and five months younger than the men. Contrary to what we have been told, their mean age at marriage both absolutely, as measured by the standard deviation, and relatively, as measured by the coefficient of variation is *more* variable than that of men. The difference in standard deviations for the ungrouped material is $2.51 \pm .93$ and for the grouped records $3.22 \pm .92$. These are 2.71 and 3.49 times their probable error, and hence perhaps significant. For the coefficient of variation, the differences by the two methods are $1.52 \pm .31$ and $1.74 \pm .31$. These are 5.69 and 4.96 times their probable errors and their significance is even more probable than those for the standard deviations.

The correlation coefficient from the grouped data by the product moment method, using the means and standard deviations given above, is

$$r_{mf} = .781 \pm .028.$$[5]

Thus on a scale of -1 to $+1$ the interdependence of mean ages of men and women is very close indeed.[6] Expressing the same relationship in terms of regression by the well known formula

$$f = \left(\bar{f} - r\frac{\sigma_f}{\sigma_m}\bar{m}\right) + r\frac{\sigma_f}{\sigma_m}m,$$

where the bars indicate population means and the sigmas population standard deviations of m = males and f = females,

$$f = -56.474 + 1.009\ m.$$

Thus we see that each month's increase in average male age is followed by a month's increase in mean female age. The fit of the straight line to the empirical means as shown in the diagram is excellent—considering the small number of the district means from which the equation is deduced.

Thus the available data show that the mean age at marriage of women instead of being less variable from district to district than that of men is actually more variable—both absolutely and relatively.

In short, there is, as far as our data go, no evidence for the assertion that while the time of marriage of men is closely dependent upon the complex of social and economic conditions that of women is practically independent of them.

We have published this note in the hope that it may suggest to some one with the opportunities of obtaining really adequate data an investigation of the problem which has several rather important points of interest.

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[5] The difference method applied to the ungrouped material gives

$$r = .763 \pm .030.$$

The difference is of no significance.

[6] Possibly, however, the relationship is in part spurious. The mean of males and females were taken on the basis of the same N, or approximately the same N, for the various districts. Data for investigating this question are not available. The point should be borne in mind by a subsequent worker.

DUPLICATE GENES

SOME interesting questions are raised by a recent article by Gregory: "On the Genetics of Tetraploid Plants in *Primula sinensis*."[1] Reciprocal crosses of two races of *P. sinensis* were made. One cross gave entirely normal results in F_2 as regards chromosome number and hereditary characters. The reciprocal cross gave an F_1 generation which was sterile with the parents and produced only a giant variety in F_2. This proved to have the tetraploid chromosome number. Experiments indicated that the genetic factors had also all been doubled, a very significant parallelism.

Gregory uses the nomenclature AAAA, AAAa, AAaa, Aaaa, and aaaa to represent all the possible conditions as regards a pair of Mendelian factors. He states that heterozygotes of the form AAAa should give gametes AA and Aa, and should produce, on selfing, the zygotes AAAA, 2AAAa and AAaa, and that the last class selfed should produce recessives. On the chromosome theory of heredity, this assumes that the four chromosomes concerned are equally likely to pair in synapsis in any of the possible ways, a very interesting phenomenon if the assumption proves correct. But it is conceivable that two independent synaptic pairs may be formed. It may be that only chromosomes from the same original race pair in synapsis. It is true that the first of the original crosses shows that the chromosomes of the two races can enter into normal mitosis and presumably into synapsis with each other. But the reciprocal cross indicates, perhaps, that in the environment of the cytoplasm of this cross, they can not enter into synapsis. If this condition continues in later generations, we should represent the zygotes as AAA′A′, AAA′a′, AaA′a′, etc. This is the way in which duplicate genes have been represented previously as by Nilsson-Ehle, East and Shull. With this representation, heterozygotes of the form AAA′a′ could never give rise to recessives after selfing for any number of generations.

Which hypothesis is true in this case could easily be determined by experiment. The published results are not sufficiently explicit on this point. If the original cross were of the type AA × a′a′, producing in F_1 Aa′, the F_2, AAa′a′, would be a homozygote on the second hypothesis, and recessives should never

[1] *Proc. Roy. Soc.*, B 87, 1914.

appear. On Gregory's hypothesis recessives should appear in later generations. On the second hypothesis, homozygous races of the types AAa'a' and aaA'A' would be obtainable, in appearance like heterozygotes. These would breed true indefinitely when selfed, but should give recessives in F_2 after crossing, as in a case proved by Nilsson-Ehle.

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June 19, 1914

NOTES AND LITERATURE

A STUDY OF DESERT VEGETATION[1]

Between three and four years ago Dr. W. A. Cannon, of the Desert Botanical Laboratory at Tucson, Arizona, visited southern Algeria in order to become acquainted with the more obvious features of the plant physiological conditions of the desert, and to make detailed studies of the root habits of certain desert plants. From Algiers the journey proceeded nearly due south about three hundred miles to Ghardaia, thence east about one hundred miles to Ouargla, and another hundred miles to Touggourt, returning through Biskra, and Batna to the northern coast. Throughout this long and wearisome journey the vegetation was studied in connection with the geographical and climatic environment and the results are brought together in a volume of somewhat more than eighty pages of text and thirty-seven plates, one of which is an outline map of the region visited.

Dr. Cannon speaks of the similarity of the flora of Algeria to that of southern Spain, France and Italy, where one is reminded of the vegetation of portions of California. Once in the desert on the way south low-growing shrubs on the plain become characteristic, including species of *Tamarix, Zizyphus* and *Artemisia.* Where water is available for irrigation, oases occur with their luxuriant vegetation of date palms, apricots, figs, mulberries, peaches, pears, oranges, as well as artichokes, beans, carrots, melons, peas, potatoes, squashes, etc. Further south the plain

[1] Botanical Features of the Algerian Sahara. By William Austin Cannon, Washington, D. C. Published by the Carnegie Institution of Washington, 1913.

is covered with small stones and pebbles and "not a tree, shrub, or herb appears to hide the bare ground. The mountains are naked rock, while the harsh outline of desert ranges and the distant low sand ridges give no evidence of plant life. But a closer examination of plain, dune and mountains reveals the presence either of living forms or of the dried remains of plants of a preceding moist season, in numbers and in kinds not at first suspected." All of which might well describe the desert conditions in our own southwest. This similarity is emphasized by the resemblance of many of the plants to those found in our Arizona deserts. Thus the "quidad" (*Acanthyllis tragacanthoides*) "has a very close resemblance to small specimens of 'ocotillo' (*Fouquieria splendens*) of the southwestern United States." And this resemblance extends to the structure of the spines and the return of the foliage after rains. It is interesting to note that the natives burn off its numerous spines, after which the stems "are eaten with avidity by camels," reminding us of the similar treatment and use of some cactuses in Arizona. Further to the south the vegetation is still more sparse and xerophytic, including *Ephedra, Retama, Haloxylon,* and among grasses, *Aristida pungens.* Near Ouargla, the southern point reached, there are places where no vegetation is present, as on the dunes, and yet on the fixed sand nearby were found *Euphorbia guyoniana, Retama retam* and *Genista saharæ.*

Much attention was given to the root habits of the plants encountered, and in the general summary which follows the account of the journey comparisons are made with the root habits of Arizona plants.

With this meager introduction we must refer the reader to the volume itself, which it is quite impossible to summarize in these pages. One thing impresses itself forcibly upon the reader, and that is that a desert is a *hungry place* in which the permanent vegetation maintains itself against plant-eating animals by a thorny or spiny protection. Yet Dr. Cannon points out that in this character of spininess the American desert plants excel those of the plants of the Sahara region.

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